Spring 1977

BREEDING AND GENETICS OF HYDROXAMATES IN ZEA MAYS L

BRYANT JEROME LONG

BREEDING AND GENETICS OF HYDROXAMATES IN ZEA MAYS L.

by

Bryant J. Long

B.S. Defiance College, 1972

M.S. University of New Hampshire, 1974

A THESIS

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Doctor of Philosophy

Graduate School

Department of Plant Science

June, 1977

This thesis has been examined and approved.

Gerald M. Dunn

Thesis director, Gerald M. Dunn, Prof. of Plant Science

Douglas G. Routley

Douglas G. Routley, Prof. of Plant Science

Lincoln C. Peirce

Lincoln C. Peirce, Prof. of Plant Science

Yun Tzu Kiang

Yun Tzu Kiang, Assoc. Prof. of Plant Science

Robert O. Blanchard

Robert O. Blanchard, Asst. Prof. of Botany and Plant Pathology

5/11/77

Date

ACKNOWLEDGMENTS

The author wishes to express his sincere thanks and appreciation to:

(1) My major advisor, Dr. Gerald M. Dunn, for his advice in these studies and criticism of the manuscript.

(2) The members of my guidance committee for their evaluation and criticism of this research and thesis, including: Drs. Douglas G. Routley, Lincoln C. Peirce, Yun Tzu Kiang, and Robert O. Blanchard.

(3) My wife, Rebecca, for her encouragement and patience throughout the course of these studies.

(4) Ms. Cathy Hendrickx for typing the manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

ABSTRACT

BREEDING AND GENETICS OF HYDROXAMATES IN ZEA MAYS L.

by

Bryant Long

Hydroxamic acids have been implicated in the resistance of maize to both insects and fungi. In this study, five selected crosses among four inbred lines were used to study the inheritance of hydroxamates in maize.

Hydroxamate concentration in the parental, F_1, F_2, and backcross generations for each cross was estimated by a rapid procedure based upon the colorimetric reaction of hydroxamates with $FeCl_3$. Variance components and heritability estimates were obtained according to the procedures formulated by Warner.

Data from the F_2 and backcross distributions indicated that hydroxamate concentration is controlled monogenically in the cross BxBx X bxbx and multigenically in the crosses bxbx X B49 and bxbx X B37. Estimates of gene number using the Castle-Wright formula indicated that hydroxamate concentration is conditioned in B49 and B37 by five and two genes, respectively. The addition of BxBx to either B49 or B37 resulted in an increased frequency of genotypes in the F_2 possessing a high hydroxamate concentration.

Additive genetic variance was the most important component of the phenotypic variance and resulted in heritability estimates ranging from 0.64 to 0.79. However, the dominance component of variance was considerably higher for crosses

involving BxBx than for the crosses bxbx X B49 and bxbx X B37. This was reflected in the high estimates of degree of dominance exhibited by the BxBx crosses.

In the same study, two cycles of simple recurrent selection were performed to increase hydroxamate concentration in maize. Five inbred lines BxBx, B49, C131A, Oh45, and R101 were chosen from an original source population of 13 inbred lines varying widely in hydroxamate concentration. These five lines possessed the highest hydroxamate concentration when analyzed by the rapid procedure. One cycle of recurrent selection increased the original population mean from 0.54 mg to 0.79 mg hydroxamates/g fresh weight. An additional cycle increased the mean to 0.93 mg. Heritability estimates (narrow sense) for the two populations were calculated as h^2 = 0.66 and h^2 = 0.54, respectively.

INTRODUCTION

The occurrence of a cyclic hydroxamate, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), was first reported in corn in 1959. DIMBOA has since been implicated in the resistance of maize to several insects and fungi. Presence of hydroxamates in maize has been associated with resistance to the European corn borer and to the corn leaf aphid. Hydroxamates have also been implicated in the resistance of wheat to stem rust and the resistance of maize to stalk rot and northern corn leaf blight. Several workers have suggested breeding for high hydroxamate concentration on the basis of these studies.

Two types of genetic control have been hypothesized for hydroxamate accumulation in maize. The first is thought to be conditioned by a single dominant gene, BxBx, which was found to be segregating 3:1 for presence or absence of hydroxamates in the F_2 from an open-pollinated ear of Gehu yellow dent. The second type of genetic control is thought to be conditioned by many genes and behaves as a quantitative character.

The objectives of the present studies were (1) to study the inheritance of cyclic hydroxamate concentration in maize; and (2) to conduct two cycles of recurrent selection for increasing hydroxamate concentration in maize.

LITERATURE REVIEW

Hydroxamates

Occurrence in Higher Plants

The cyclic hydroxamate 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) was first reported in maize (Zea mays L.) and wheat (Triticum aestivum L.) in 1959 (72). Presence of the demethoxyl analog has since been demonstrated in rye seedlings where it similarly exists as a glucoside in intact tissue (71). Mechanical injury or cellular disruption triggers the enzymatic hydrolysis of the glucoside releasing the aglucone DIMBOA. The reactions responsible for the formation of hydroxamates in corn, wheat, and rye seedlings are shown in Fig. 1.

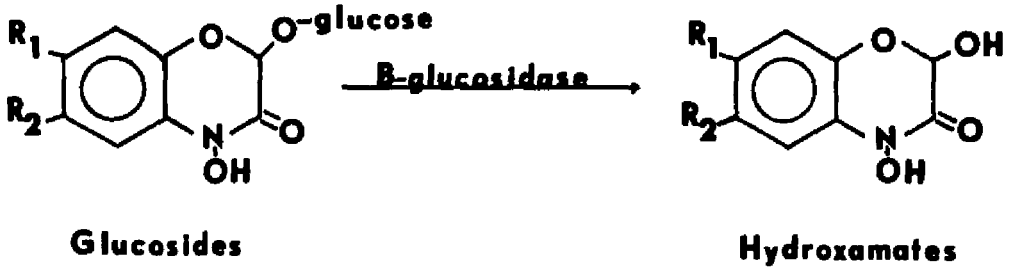


Figure 1. Formation of hydroxamates in corn and wheat ($R_1 = OCH_3$, $R_2 = H$) and rye ($R_1 = R_2 = H$).

Quantitative Analysis of Hydroxamates

Four procedures have been adopted for quantitative determination of hydroxamates in plant tissue. They are the isotope dilution technique (44), the direct measurement of benzoxazolinones by UV absorbance at 285 nm (4), spectrofluorometry of benzoxazolinones (7), and the colorimetric

procedure using ferric chloride reagent (29). All four procedures offer high sensitivity and excellent separation of high and low lines. However, the isotope dilution technique requires large amounts of tissue, a source of ^{14}C-benzoxazolinones, and it is time consuming. The three spectrophotometric procedures are simpler but are relatively non-specific in nature. Recently a rapid procedure has been developed for estimating hydroxamate concentration in maize (49) based upon the colorimetric procedure of Hamilton.

Biological Activity

DIMBOA has been implicated in resistance of plants to several insects and pathogens. In 1966, Klun and Brindley showed a positive correlation between concentrations of MBOA in dried whorl tissue and resistance to the European corn borer (44). However, the same workers discounted MBOA as a primary resistance factor as it failed to cause mortality when incorporated into artificial diets fed to borers.

A later study demonstrated that the immediate precursor, DIMBOA, was active in the resistance of corn to the first brood larvae of the European corn borer (45). Incorporation of DIMBOA into an artificial diet at a concentration of 0.32 mg/g diet caused over 25% borer mortality. In a similar study, a highly significant correlation ($r = 0.83$) was found between concentrations of DIMBOA in whorl tissue of eleven maize inbreds and resistance to the European corn borer (46).

Long, et al. used bioassay and field experiments to test the relationship between hydroxamate concentration and

resistance to the corn leaf aphid (Rhopalosiphum maidis (Fitch)) (51). In the bioassay, various concentrations of DIMBOA were added to an artificial diet fed to corn leaf aphids. DIMBOA concentrations of 0.1, 0.25, and 0.5 mg/g diet caused 5.1, 12.8, and 20.8% mortality, respectively. In field trials, twelve inbred lines were evaluated for corn leaf aphid resistance under natural infestation. Cyclic hydroxamate concentration in a separate set of the same inbreds was estimated by a rapid procedure based upon the colorimetric reaction of hydroxamates with ferric chloride. A highly significant correlation ($r = 0.72$) was obtained between these two traits.

The biological activity of hydroxamic acids in resistance to plant diseases has also been studied. Elnaghy and Linko showed that rust resistant cultivars of wheat, Khapli and Justin, possessed a higher concentration of DIMBOA than the susceptible cultivar Little Club (20). Extracts of Khapli containing the aglucone completely inhibited rust development while extracts from Little Club had little effect. In another study Elnaghy and Shaw analyzed five cultivars of wheat, used as differentials in race identification, for hydroxamate concentration (21). They found a highly significant negative correlation between concentrations of hydroxamates and percentage of rust races attacking the cultivars. Knott and Kumar similarly demonstrated a highly significant correlation ($r = 0.88$) between hydroxamate concentration in six cultivars and resistance to stem rust (47). However,

they observed that the addition of single resistance genes to a cultivar did not change hydroxamate content.

DIMBOA has also been shown to be a factor in resistance of corn to stalk rot (5). Glycoside content of stalk rot resistant tissues was significantly higher than that of susceptible tissues based upon the analysis of four inbred lines.

Anglade and Molot demonstrated a highly significant correlation between hydroxamate concentration and resistance of maize inbreds to northern corn leaf blight caused by Helminthosporium turcicum (2). They postulated that resistance was due to high concentrations of MBOA found in resistant lines.

Couture et al. studied the role of cyclic hydroxamic acids and resistance of maize to H. turcicum (14). They observed that lines deficient in hydroxamates exhibited a significantly higher percent leaf infection than normal lines. In the same study a bioassay was performed to test toxicity of DIMBOA on germinating spores of H. turcicum. Inhibition of spore germination was nearly complete at DIMBOA concentrations above 6 ppm.

In a similar study, a set of 13 inbred lines of corn was used to determine the relationship between concentrations of DIMBOA and resistance to northern corn leaf blight (50). A significant negative correlation ($r = -0.61$) was demonstrated between concentrations of hydroxamates and percent leaf infection.

Inheritance of DIMBOA in Maize

Hamilton, in 1964, studied the inheritance of hydroxamates in maize seedlings (30). He used a qualitative test for hydroxamates to score seedlings from individual ears resulting from inbreeding an open-pollinated heterozygous ear of Gehu yellow dent. The presence of DIMBOA or its glucoside was indicated by a blue colored chelate formed when a root tip was crushed on filter paper impregnated with 0.1M $FeCl_3$ solution. Seeds deficient in hydroxamates gave no reaction. One S_1 ear, designated 59C32-1, segregated 3:1 for high versus low hydroxamate seedlings. The DIMBOA deficient seeds derived from the original S_1 ear when self pollinated, produced only deficient seedlings. Another selected ear of Gehu yellow dent gave only high hydroxamate progeny through four generations of self pollination. When these S_3 plants were crossed with homozygous low hydroxamate plants all high hydroxamate progeny were produced. Upon selfing a 3:1 ratio was obtained for high versus low hydroxamate seedlings. These results were later confirmed by Couture *et al.* who designated the gene conditioning DIMBOA production in maize as *BxBx* (13).

In 1970 Klun *et al.* presented evidence for quantitative inheritance of DIMBOA (46). In this study a diallel set of eleven maize inbreds was used to compare concentrations of DIMBOA and resistance to the European corn borer. Analysis for DIMBOA content produced approximately a ten to one ratio between high and low lines. From the analysis of variance

the sum of squares for general combining ability accounted for nearly 91% of the variation among hydrids in respect to DIMBOA concentration. Selection for resistance to the European corn borer on the basis of DIMBOA content was therefore considered feasible.

Components of Phenotypic Variance

The partitioning of the phenotypic variance (Vp) into the two components V_G (genetic variance) and V_E (environmental variance) had its beginnings in the work of Johannsen (41) and East (17). However, it was not until 1918 that R. A. Fisher demonstrated that the total genetic variance could be divided into the three fractions $V_A + V_D + V_I$ representing additive, dominance, and epistatic variances, respectively (23). He proposed that the dominance component of variance represented the summation of deviations of a heterozygous hybrid from the midparental value. Similarly, epistatic variance comprised interactions between genes at different loci resulting in deviations from the additive scheme. The summation of the additive gene effects produced by genes without dominance (additive genes) and by additive contributions of genes with dominance or epistasis was defined as V_A.

Variance components have proven especially useful in providing estimates of heritability (63, 64, 66, 69, 73) and genetic advance (6, 11, 48, 75). Variance components can also be used as aids in choosing the proper breeding procedure, in selecting genetically promising populations, and in deciding whether enough genetic variation is present for selection to be worthwhile (16).

Several methods have been used to calculate variance components. Charles and Smith (10) and Powers (62) were among the first to separate the genetic from the total phenotypic variance by estimating environmental variances from an

analysis of variance and from relations between means and variances. In a similar fashion, Lush (54) and Panse (58) studied genetic variation and further subdivided it into additive and non-additive variation. Lush, in particular, proposed using the ratio of the additive genetic component of variance to the total variance as a measure of the degree of heritability.

One of the simplest techniques was developed in 1952 by Warner for partitioning phenotypic variances (74). In this procedure estimates of variance components were obtained utilizing the individual variances of the P_1 (parent one), P_2 (parent two), F_1, F_2, and BC_1 and BC_2 (backcrosses of the F_1 X P_1 and F_1 X P_2, respectively). The estimate of the additive genetic variance was then utilized in calculating heritability estimates for a series of eleven characters from a cross of two inbred lines of corn. These studies indicated a significant dominance component in the inheritance of kernel yield, diameter of ear, and kernel number. Genetic variance appeared to be predominantly additive for traits such as kernel row number and total kernel number.

The procedure formulated by Warner has also been applied to several other inheritance studies. Barnett and Caviness used Warner's technique to study the inheritance of hydrocyanic acid (HCN) production in sorghum X sudangrass crosses (3). High HCN production was found to be partially dominant to low HCN production. However considerable additive gene effects seemed to be involved. In another study Liang and

Walter used the procedure in obtaining heritability estimates for a number of agronomic characters in grain sorghum (48). Heritabilities of grain yield and kernel number were of lower magnitude than those for head weight, kernel weight, stalk diameter, plant height, and germination percentage. Mock and Schuetz similarly used Warner's procedure in studying the inheritance of tassel branch number in maize (56). Data from the analysis indicated that the majority of the genetic variation for tassel branch number was due to additive gene action.

Several other techniques have been developed since 1952 for estimating variance components under different situations. Of these procedures parent offspring regressions as outlined by Kempthorne (43) and Falconer (22) and diallel crossing systems based upon the theories formulated by Hayman (32), Griffing (26), Jinks (39, 40), and others have been most widely used in agronomic studies.

Recurrent Selection

Hayes and Garber (31) in 1919 and East and Jones (18) in 1920 first suggested a breeding scheme whereby selected individuals were intercrossed as a means of concentrating favorable gene combinations for a desired character. They advocated that this technique would result in improvement of the mean performance of a population with a minimal loss of genetic variation. However, it was not until Jenkins (36) and Hull (34) specifically outlined this type of breeding system that the method acquired the name, recurrent selection.

Currently four types of recurrent selection systems are recognized. Allard categorized these types as simple recurrent selection, recurrent selection for general combining ability, recurrent selection for specific combining ability, and reciprocal recurrent selection (1).

Simple recurrent selection is based primarily on the breeding methods formulated by East and Jones (18). Their procedure consisted of self-pollinating plants from an original source population, intercrossing selected S_1 plants in all combinations, and utilizing the resulting intercross population as source material for additional cycles of selection and intercrossing. No test crosses were used in this procedure.

Convincing evidence on the effectiveness of simple recurrent selection was first presented by Sprague and Brimhall in studies directed toward increasing oil content in corn

(67). They compared the effectiveness of two cycles of recurrent selection versus selection within inbred lines in increased oil percentage from 4.2 to 7.0%. This was about 2.6 times as effective as the selfing series.

Simple recurrent selection has similarly been utilized in concentrating genes for resistance to northern corn leaf blight (37). In this study it was found that two generations of recurrent selection were sufficiently effective to be warranted in nearly all groups of progenies tested. However, little improvement was obtained from a third cycle of recurrent selection.

Simple recurrent selection has also been utilized in breeding for resistance to the European corn borer in maize (60). Two cycles of recurrent selection in five synthetic varieties shifted the frequencies of resistance genes to a high level. Three cycles produced essentially borer-resistant varieties. Similar results have been obtained in studies conducted by other workers using simple recurrent selection to increase resistance of maize to stalk rot (38), to stalk lodging (70), and to corn stunt (65).

The second type of recurrent selection, involving selection for general combining ability, developed as a direct outgrowth of studies of early testing formulated by Jenkins in 1935 (35). The procedure is basically the same as simple recurrent selection except that S_0 plants selected from the source population are selfed and also crossed to a heterozygous tester for evaluation of general combining ability.

Jenkins advocated that tests of general combining ability offer greater promise of producing high yielding individuals than lines drawn from the population on the basis of visual selection alone.

One of the first successful evaluations of recurrent selection for general combining ability in maize was conducted by Lonquist in 1951 (52). In this study selections were made for high and low combining lines from an original population of the variety Krug Yellow Dent. One cycle of recurrent selection separated the original population into two distinct groups differing significantly in combining ability.

Later studies have similarly demonstrated the importance of top crossing to a tester with a broad genetic base for early evaluation of superior genetic material (15, 53).

Other workers however have felt that dominant genes in the tester may actually be masking genetic differences among the lines being evaluated. Several studies demonstrated that evaluation of S_1 lines *per se* was a better method of estimating the genetic potential of S_o plants than the use of testcross evaluation (8, 24, 25).

The third type of recurrent selection, based upon specific combining ability, was proposed by Hull in 1945 (34). The objective of Hull's procedure was to produce lines that would combine well with a narrow base genetic tester. Commercial maize hybrids could therefore be generated rapidly if the tester was a seed parent already in commercial use.

Sprague *et al.*, using the inbred line Hy as tester, demonstrated 6.7% and 20.0% yield gains after two cycles of

recurrent selection for specific combining ability in the two maize populations 'Lancaster' and 'Kolmeier' (68). Similarly, Penny et al. obtained yield gains of 8.4% in an open-pollinated variety 'Alph' and 0.2% for the F_2 of WF9 X B7 after two cycles of recurrent selection utilizing B14 as tester (59).

Horner et al. recently evaluated six lines selected in the fifth cycle of recurrent selection for specific combining ability with the single cross F44 X F6 (33). The six lines were evaluated as pollen parents individually (three-way crosses), in single cross combinations (double crosses), and as a six line synthetic (top cross). Although no statistical differences in average grain yield were found, it was considered that the top cross could be released quickly and economically and that its use in commerical hybrids would be justified.

In another study five cycles of recurrent selection for specific combining ability were utilized in an attempt to produce high yielding maize lines resistant to the corn earworm (76). Although a relatively high degree of resistance was attained through the first two cycles of recurrent selection, progress slowed considerably in later cycles. It was suggested that either a change in the method for measuring earworm injury or the use of a more susceptible tester would make further selection possible.

The fourth type of recurrent selection was formulated in 1949 by Comstock et al. for selection of both general and specific combining ability (12). They termed the procedure

reciprocal recurrent selection since two source populations are involved, each of which serves as tester for the other. Using this technique selected lines from each population are eventually crossed to produce new hybrids for commercial use.

In the same study these workers compared the theoretical efficiency of reciprocal recurrent selection to recurrent selection for general combining ability and recurrent selection for specific combining ability. Comparisons were made on the improvement limit expected by each method under three levels of dominance: partial dominance, full dominance, and overdominance. In all cases reciprocal recurrent selection appeared to be either equal or superior to the other types of recurrent selection.

Subsequent studies by several other workers have reaffirmed the usefulness of reciprocal recurrent selection for improving yields in maize (27, 28, 42, 57, 61).

MATERIALS AND METHODS

Description of Inbred Lines

All materials except the BxBx and bxbx genotypes were obtained from Dr. A. R. Hallauer, research geneticist, Iowa State University. The Iowa materials are all highly inbred lines.

The BxBx and bxbx genotypes came from Dr. R. M. Couture's M.S. thesis materials from the University of New Hampshire, originally from Dr. R. H. Hamilton of the Pennsylvania State University. The original line, 59C32-1, was segregating 3:1 for the normal (BxBx) versus the deficient mutant (bxbx) on the basis of a qualitative test for presence or absence of hydroxamates (30). The BxBx and bxbx genotypes have been self-fertilized six to seven generations each.

Inheritance Studies

Five selected crosses BxBx X bxbx, BxBx X B49 (high multigenic DIMBOA line), BxBx X B37 (low multigenic DIMBOA line), bxbx X B49, and bxbx X B37 were used in the inheritance study. Each parent and the corresponding F_1, F_2, BC_1 (F_1 X P_1), and BC_2 (F_1 X P_2) were analyzed for hydroxamate concentration using the rapid procedure (49).

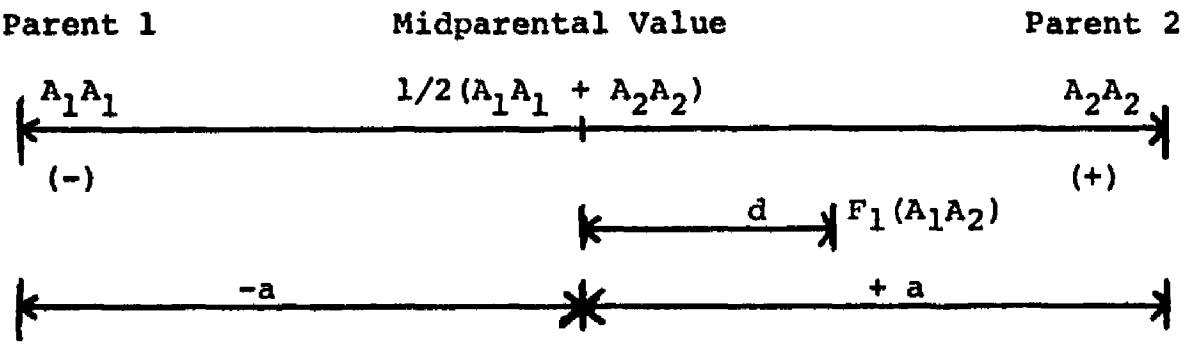
The procedure consisted of removing a 0.1 to 0.2 g section of tissue from the outer layers of the lower stem of seedlings 14-16" high (5th to 6th leaf stage). The samples of stem tissue were placed in plastic vials and frozen overnight. Subsequent thawing of the tissue allowed the

B-glucosidase to hydrolyze the glucoside and release DIMBOA. Crude extracts were prepared by crushing the tissue with a mortar and pestle in 1.0 ml of a solution containing equal volumes of 95% ethanol and 0.1 N HCl. Two washings of the mortar and pestle brought the final volume to 1.9 ml. The extract was centrifuged and decanted into a cuvette to which was added 0.1 ml of 0.1N $FeCl_3$. Absorbance values were obtained and concentrations determined from a standard curve prepared from DIMBOA isolated from etiolated corn seedlings and purified by repeated crystallization (72).

The rapid procedure based upon the ferric chloride reaction is not specific for DIMBOA. Although DIMBOA is by far the major hydroxamate in Zea mays, it is likely that other related hydroxamates are present in trace quantities. For this reason, the data in this thesis are expressed as total hydroxamate concentration rather than DIMBOA concentration.

Approximately fifty plants of each parent and F_1 were analyzed for hydroxamates. Similarly, hydroxamate concentration was determined in about 100 plants of each backcross (BC_1 and BC_2) and 250 plants of each F_2.

Estimates of genetic effects and genetic variance components were obtained using the procedure outlined by Warner (74). The model upon which Warner bases his technique is the same as that described by Mather (55) and Fisher (23):



In this model +a and -a represent the summation of the contributions of the loci where the alleles contribute a positive and negative influence on the phenotype, respectively (additive portion). Therefore the phenotypic difference between homozygotes equals a + a or 2a. The deviations of the F_1 from the midparental value is an indication of dominance and is symbolized by d. When d = a, dominance is complete. When d = 0, dominance is absent, and all genetic variance is presumably additive. However, when more than one locus is involved, dominance may be occurring in a plus and minus direction and exactly counter-balancing one another.

Additive and dominance components of variance can be expressed in terms of a and d. For a single locus (A_1A_2) segregating in the F_2, three genotypes are produced in the following proportions:

$$1/4A_1A_1 : 1/2A_1A_2 : 1/4A_2A_2$$

These values, when considered as a departure from the midparental mean in accordance with the model, yield A_1A_1 = -a, A_1A_1 = d, and A_2A_2 = +a. The average F_2 mean is then $1/4\ (-a) + 1/2(d) + 1/4(+a) = 1/2d$.

The variance contributed by each genotype is its squared

deviation from the mean multiplied by its frequency ($f(x - \bar{x})^2$) such that the F_2 genotypic variance is:

$$1/4(a-1/2d)^2 + 1/2(d-1/2d)^2 + 1/4(a-1/2d)^2$$

$$= 1/4(a^2 + ad + 1/4d^2) + 1/2(1/4d^2) + 1/4(a^2 - ad + 1/4d^2)$$

$$= 1/2a^2 + 1/4d^2$$

Designating $a^2 = A$ and $d^2 = D$ the total F_2 variance becomes $1/2A + 1/4D + E$ where $1/2A = V_A$ and $1/4D = V_D$ and E = the environmental component.

It can similarly be demonstrated that the variance of each backcross generation is $1/4A + 1/4D + E$ and that the combined variances of the backcross generations (BC_1 and BC_2) yields $1/2A + 1/2D + 2E$. The variance components for measurements in different generations then becomes:

$$V_{P1} = E$$
$$V_{P2} = E$$
$$V_{F1} = E$$
$$V_{F2} = 1/2A + 1/4D + E$$
$$V_{BC1} = 1/4A + 1/4D + E$$
$$V_{BC2} = 1/4A + 1/4D + E$$
$$V_{BC1} + V_{BC2} = 1/4A + 1/2D + 2E$$

In the present study the environmental variance was obtained from the average of P_1, P_2, and F_1 since each was considered genetically uniform. The additive component of variance, $1/2A$, was estimated by multiplying V_{F2} by two and subtracting from it the combined backcross variances, thus eliminating the dominance and environmental components. By subtracting the additive and environmental variances from

the total phenotypic variance, an estimate of the dominance variance was obtained. The degree of dominance was calculated as $\sqrt{\frac{4V_D}{2V_A}}$. Heritability estimates (narrow sense) were calculated according to the equation $h^2 = \frac{1/2A}{1/2A + 1/4D + E}$. Estimates of gene number were calculated according to Castle's formula $N = \frac{D^2}{8(V_{F2} - V_{F1})}$ where N = gene number, D = the difference between the parental means, and V_{F1} and V_{F2} = the phenotypic variances of the F_1 and F_2, respectively (8a). All values were transformed to logarithms in order to satisfy the assumptions of scaling upon which the analysis is based.

Recurrent Selection

The five lines BxBx, B49, C131A, Oh45, and R101 were chosen for use in the simple recurrent selection program from an original source population of 13 inbred lines varying widely in hydroxamate content. These five lines possessed the highest hydroxamate content based upon an analysis by the rapid procedure.

The selected inbred lines were grown in the greenhouse for interpollination in the spring of 1974. Pollen was collected from each of these inbreds, weighed and mixed in approximately equal proportions, and placed on the silks of the same inbred lines. Seed was then harvested from the intercross population, bulked, and a random sample planted in the field the following summer. Approximately 300 plants

were self-pollinated and the bulked seed saved.

A portion of this seed was planted in the greenhouse in 12" clay pots in the fall of 1975. This population consisted of about 250 plants which were analyzed non-destructively for hydroxamate concentration using the rapid procedure on plants 16-18" high. Fifteen plants having the highest concentration of hydroxamates were selected to make up the next intercross population. The procedure thus far constituted one cycle of simple recurrent selection. An additional cycle was performed in the summer and fall of 1976.

Heritability estimates (narrow sense) were obtained according to the equation $h^2 = \frac{X_o - \overline{X}}{X_p - \overline{X}}$ where X_o = mean of the offspring of the selected individuals, X_p = mean of individuals selected from the original source population, and $\overline{X}$ = mean of the original source population.

RESULTS AND DISCUSSION

Inheritance Studies

Five selected crosses, BxBx X bxbx, bxbx X B49 (high multigenic line), bxbx X B37 (low multigenic line), BxBx X B49, and BxBx X B37 were analyzed in the P_1, P_2, F_1, F_2, BC_1, and BC_2 generations for hydroxamate concentration using the rapid procedure.

Ranges, means, and variances for parents and progenies from the cross BxBx X bxbx are given in Table 1. Frequency distributions for the parental, F_1, F_2, BC_1, and BC_2 populations for hydroxamate concentration are presented in Fig. 2. The parents differed widely in hydroxamate concentration, with BxBx averaging 0.290 mg and bxbx averaging 0.034 mg hydroxamates/g fresh weight. Plants in the F_1 and F_2 generations averaged 0.221 and 0.192 mg, respectively. These values are substantially higher than the midparental value of 0.162 mg and indicate the effects of dominance. Backcrosses of the F_1 to each parent resulted in concentrations of hydroxamates that were nearly intermediate to the parental extremes.

Variances for hydroxamate concentration were considerably larger for the F_2, F_3, BC_1, and BC_3 generations than for the non-segregating generations. This is evidence of genetic variability for this character.

Data presented in Fig. 2 indicated that there was a high degree of phenotypic dominance for hydroxamate concentration in the cross BxBx X bxbx. This dominance was

Table 1. Ranges, means, and variances for hydroxamate concentration in parents and progenies from the cross BxBx X bxbx.≠

Population	No. of Plants	Range	Mean	Variance
bxbx	51	0.009 - 0.053	0.034	0.000149
BxBx	48	0.243 - 0.337	0.290	0.000606
F_1	50	0.184 - 0.279	0.221	0.000448
F_2	241	0.009 - 0.330	0.192	0.008601
F_3	133	0.025 - 0.324	0.190	0.009320
BC_1≠	113	0.004 - 0.274	0.142	0.008292
BC_2≠	107	0.199 - 0.344	0.258	0.002080

≠Original data transformed to logarithms for calculation of ranges, means, and variances.

≠BC_1 and BC_2 = backcrosses of the F_1 to bxbx and BxBx, respectively.

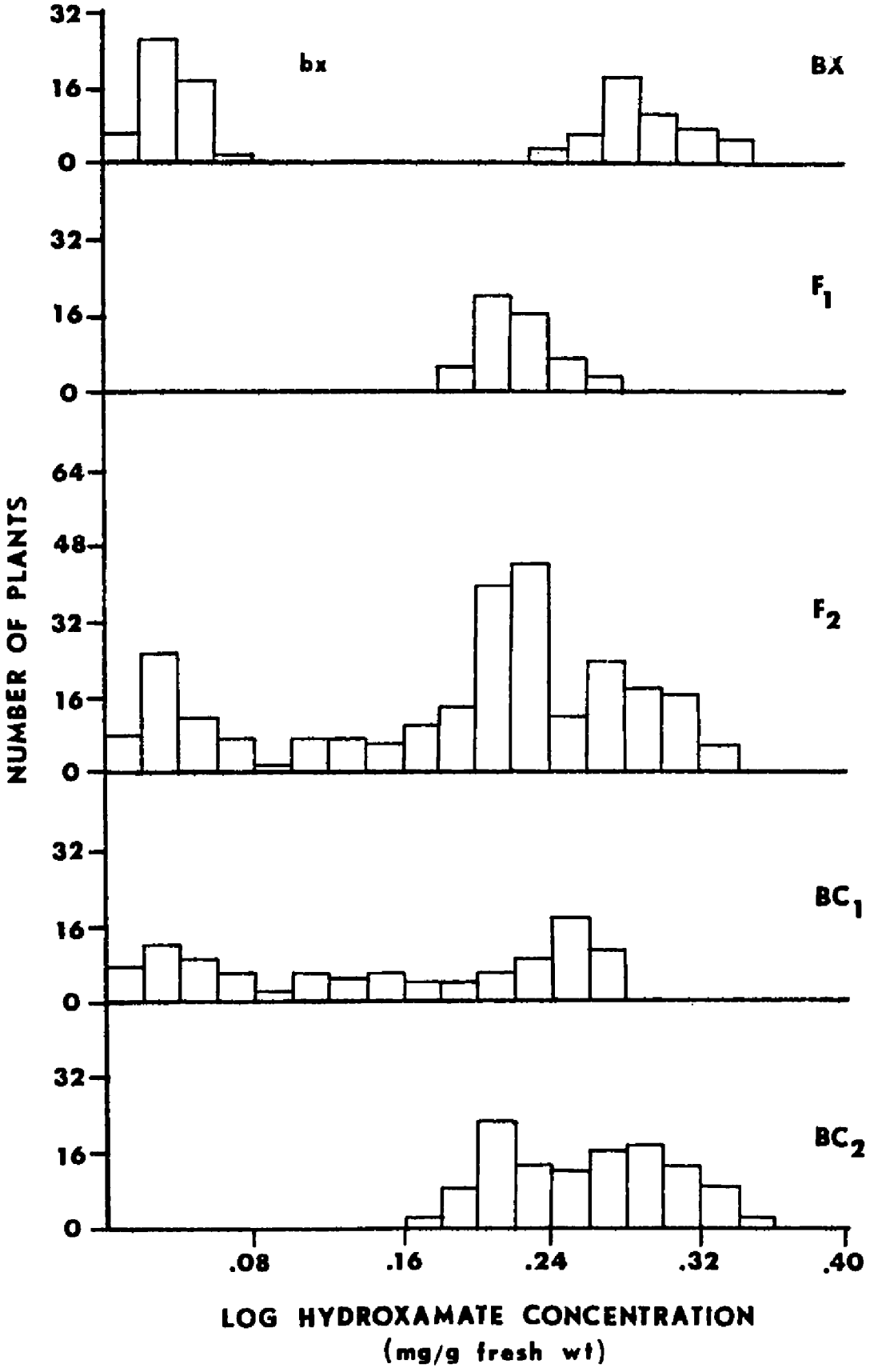


Figure 2. Frequency distributions for the parental F_1, F_2, BC_1, and BC_2 populations for hydroxamate concentration from the cross BxBx X bxbx.

revealed by the frequency distribution of the F_1, F_2, BC_1, and BC_2. The distribution of the F_2 generation appeared trimodal with the first mode ranging from about 0.00 to 0.08 mg, the second mode from about 0.16 to 0.30 mg, and the third mode from about 0.22 to 0.34 mg. The ranges for these classes were similar to the parental and F_1 populations. When hydroxamate concentration was considered as a qualitative character and placed into discrete classes, a good fit was obtained to a 1:2:1 ratio in the F_2 and a 1:1 ratio in backcrosses to either parent. Data obtained in the F_3 generation, although not shown graphically, tended to support the hypothesis that a single partially dominant gene conditions much of the hydroxamate concentration in this cross. It is also possible that minor genes and/or modifier genes may affect hydroxamate content in BxBx X bxbx.

Ranges, means, and variances, for the parents and progenies from the cross bxbx X B49 are given in Table 2. Frequency distributions for parental, F_1, F_2, BC_1, and BC_2 populations for hydroxamate concentration are presented in Fig. 3. As with BxBx X bxbx, both parents differed widely in hydroxamate concentration with bxbx averaging 0.034 mg and B49 averaging 0.326 mg hydroxamates/g fresh weight. The F_1 and F_2 means of 0.220 and 0.185 mg, respectively, were nearly intermediate to the parental extremes. The possibility of some dominance effects was indicated by the slight deviation of the F_1 and F_2 means from the midparental

Table 2. Ranges, means and variances for hydroxamate concentration in parents and progenies from the cross bxbx X B49.≠

Population	No. of Plants	Range	Mean	Variance
bxbx	51	0.009 - 0.053	0.034	0.000149
B49	49	0.264 - 0.356	0.326	0.000406
F_1	50	0.161 - 0.258	0.220	0.000360
F_2	245	0.065 - 0.303	0.189	0.002314
BC_1≠	96	0.049 - 0.225	0.141	0.001850
BC_2≠	104	0.201 - 0.322	0.271	0.000830

≠ Original data were transformed to logarithms for calculation of ranges, means and variances.

≠ BC_1 and BC_2 = backcrosses of the F_1 to bxbx and B49, respectively.

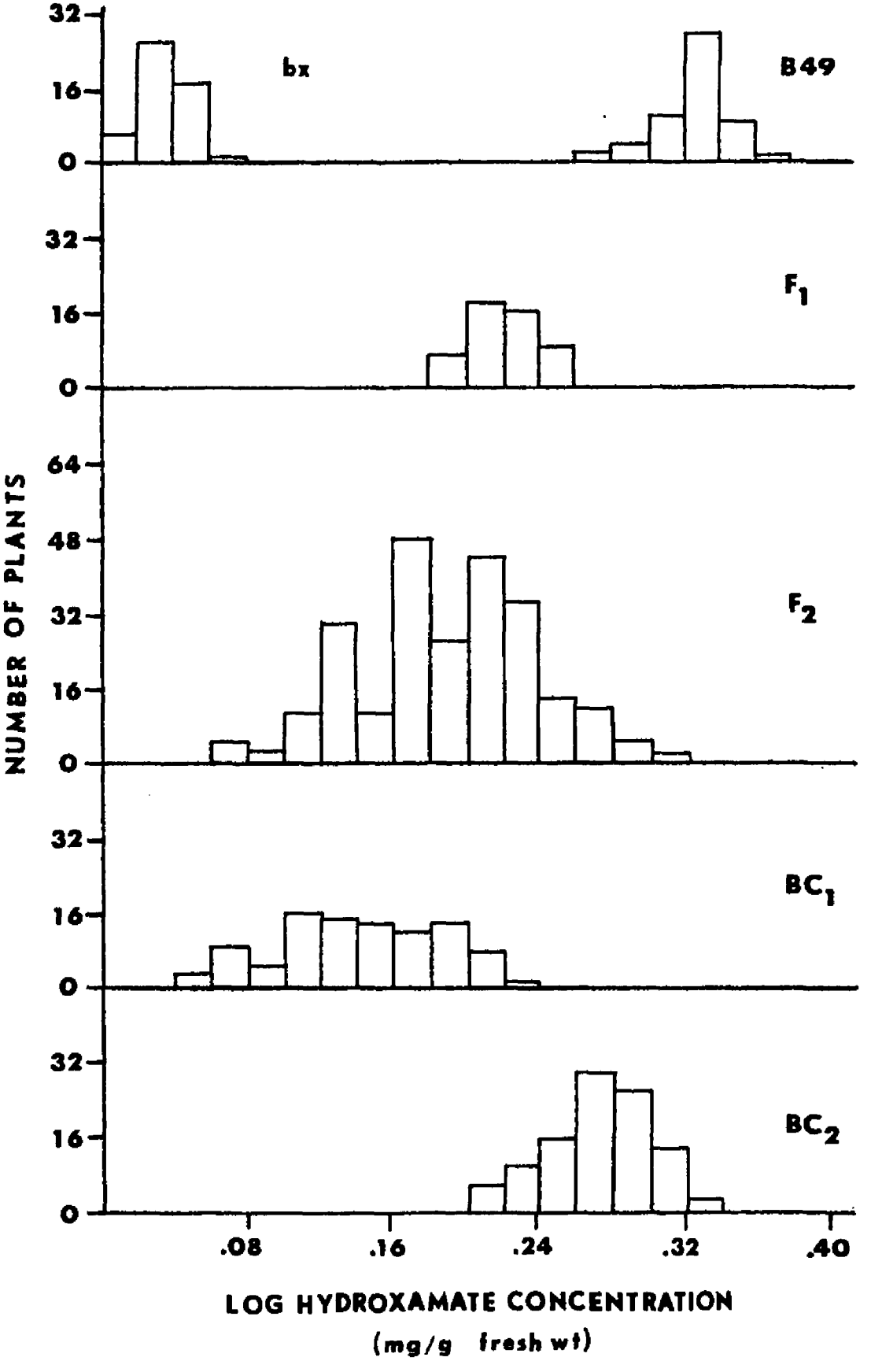


Figure 3. Frequency distributions for the parental, F_1, F_2, BC_1, and BC_2 populations for hydroxamate concentration from the cross bxbx X B49.

value of 0.180 mg. Mean concentrations of hydroxamates in each backcross (BC_1 = 0.141 mg and BC_2 = 0.271 mg) closely approximated the midparental values of 0.127 and 0.273 mg, respectively. Variances for the F_2 and backcross populations were considerably higher than the non-segregating populations but proportionally lower than corresponding generations from the cross BxBx X bxbx.

The frequency distributions for the F_2, BC_1, and BC_2 generations were continuous and appeared to follow a normal distribution curve. It was impossible to divide hydroxamate concentration in the F_2 of bxbx X B49 into discrete classes as was the case for BxBx X bxbx. From these data it appears that hydroxamate concentration is controlled in bxbx X B49 by many genes having a small but cumulative effect. It is hypothesized that B49 does not possess any one gene with an effect comparable to BxBx. Estimates of gene number using the Castle-Wright formula indicated that 5-6 genes condition hydroxamate concentration in the cross bxbx X B49.

The genetic behavior of bxbx with B37 was quite similar in pattern to its reaction with B49 (Table 3 and Fig. 4). Both parents exhibited low mean concentrations of hydroxamates (0.034 and 0.125 mg for bxbx and B37, respectively). Concentrations of hydroxamates in the F_1 and F_2 (0.091 and 0.080 mg) were close to the midparental value of 0.079 mg. Backcross means BC_1 = 0.059 mg and BC_2 = 0.012 mg were similarly in close agreement with the midparental values

Table 3. Ranges, means, and variances for hydroxamate concentration in parents and progenies from the cross bxbx X B37.≠

Population	No. of Plants	Range	Mean	Variance
bxbx	49	0.009 - 0.053	0.034	0.000149
B37	50	0.097 - 0.158	0.125	0.000241
F_1	50	0.065 - 0.111	0.091	0.000230
F_2	239	0.025 - 0.158	0.080	0.000682
BC_1≠	97	0.004 - 0.140	0.059	0.000431
BC_2≠	107	0.049 - 0.153	0.109	0.000464

≠ Original data were transformed to logarithms for calculation of ranges, means, and variances.

≠ BC_1 and BC_2 = backcrosses of the F_1 to bxbx and B37, respectively.

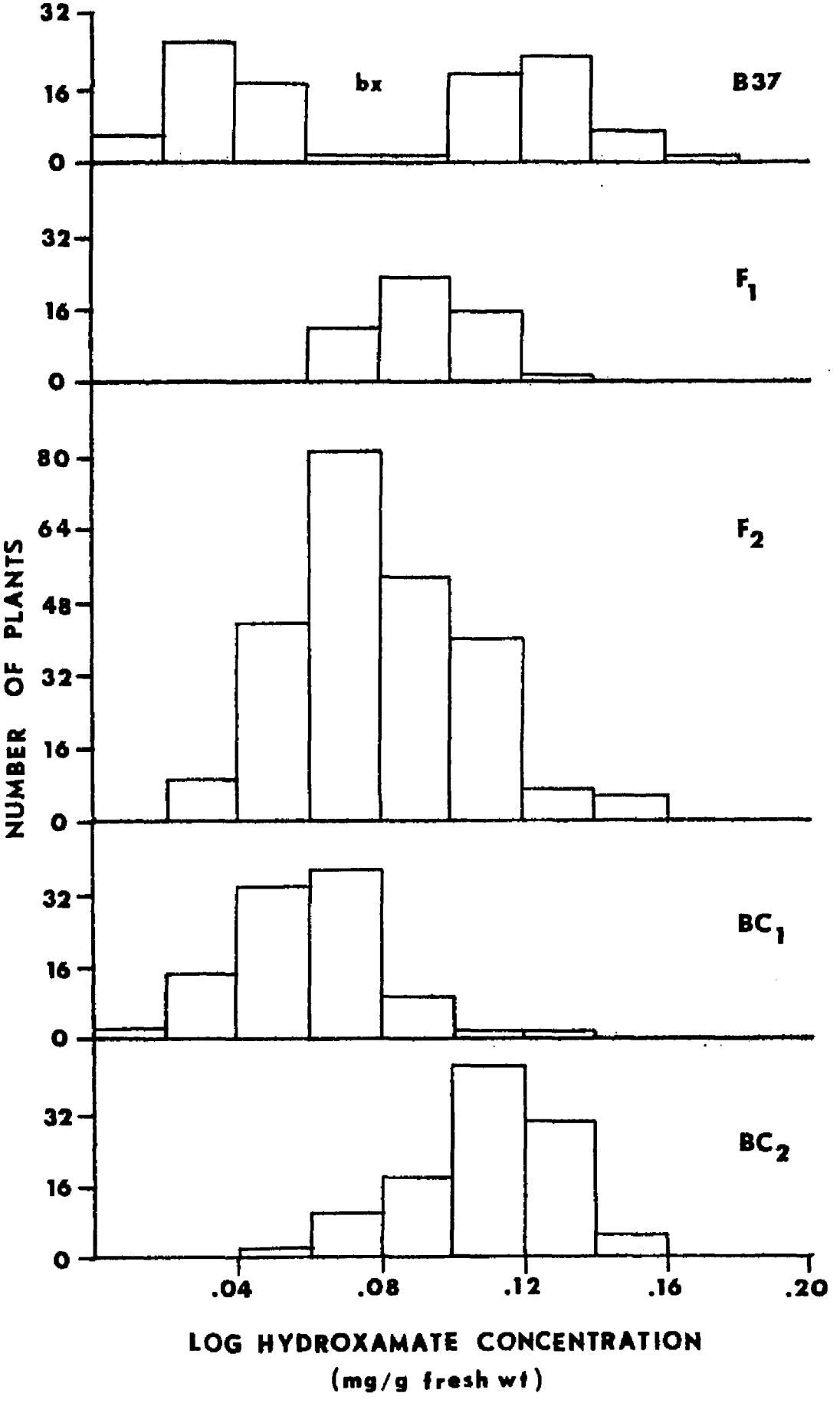


Figure 4. Frequency distributions for the parental, F_1, F_2, BC_1, and BC_2 populations for hydroxamate concentration from the cross bxbx X B37.

0.062 mg and 0.110 mg, respectively.

Variances in the F_2, BC_1, and BC_2 were considerably larger than the parental and F_1 generations but even smaller than those for bxbx X B49. This was probably due to the low amounts of hydroxamates exhibited by each parent.

As with the cross bxbx X B49, the frequency distributions for the F_2, BC_1, and BC_2 populations were continuous and normally distributed. These data indicate that hydroxamate concentration in B37 is probably controlled by relatively few genes with little or no dominance effects. The estimation of gene number using the Castle-Wright formula indicated that two genes condition hydroxamate concentration in the cross bxbx X B37.

Ranges, means, and variances for the parents and progenies from the cross BxBx X B49 are given in Table 4. Frequency distributions for hydroxamate concentration in the various generations are presented in Fig. 5. Both parents exhibited high mean concentrations of hydroxamates (0.290 mg and 0.326 mg, respectively). Mean concentration of hydroxamates in the F_1 was nearly intermediate to the parental extremes. This intermediate value may have resulted from the addition of several polygenes from B49 to the incompletely dominant BxBx genotype. Although the mean concentration of hydroxamates in the F_2 was also intermediate to the parents, the frequency distribution was highly skewed to the right. This departure from normality may similarly reflect the influence of BxBx on the multigenic expression of hydroxamate

Table 4. Ranges, means, and variances for hydroxamate concentration in parents and progenies from the cross BxBx X B49.≠

Population	No. of Plants	Range	Mean	Variance
B49	49	0.265 - 0.356	0.326	0.000406
BxBx	48	0.243 - 0.337	0.290	0.000606
F_1	50	0.299 - 0.354	0.315	0.000365
F_2	242	0.111 - 0.375	0.275	0.003660
BC_1≠	102	0.130 - 0.384	0.282	0.002976
BC_2≠	104	0.212 - 0.382	0.290	0.001910

≠ Original data were transformed to logarithms for calculation of ranges, means, and variances.

≠ BC_1 and BC_2 = backcrosses of the F_1 to B49 and BxBx, respectively.

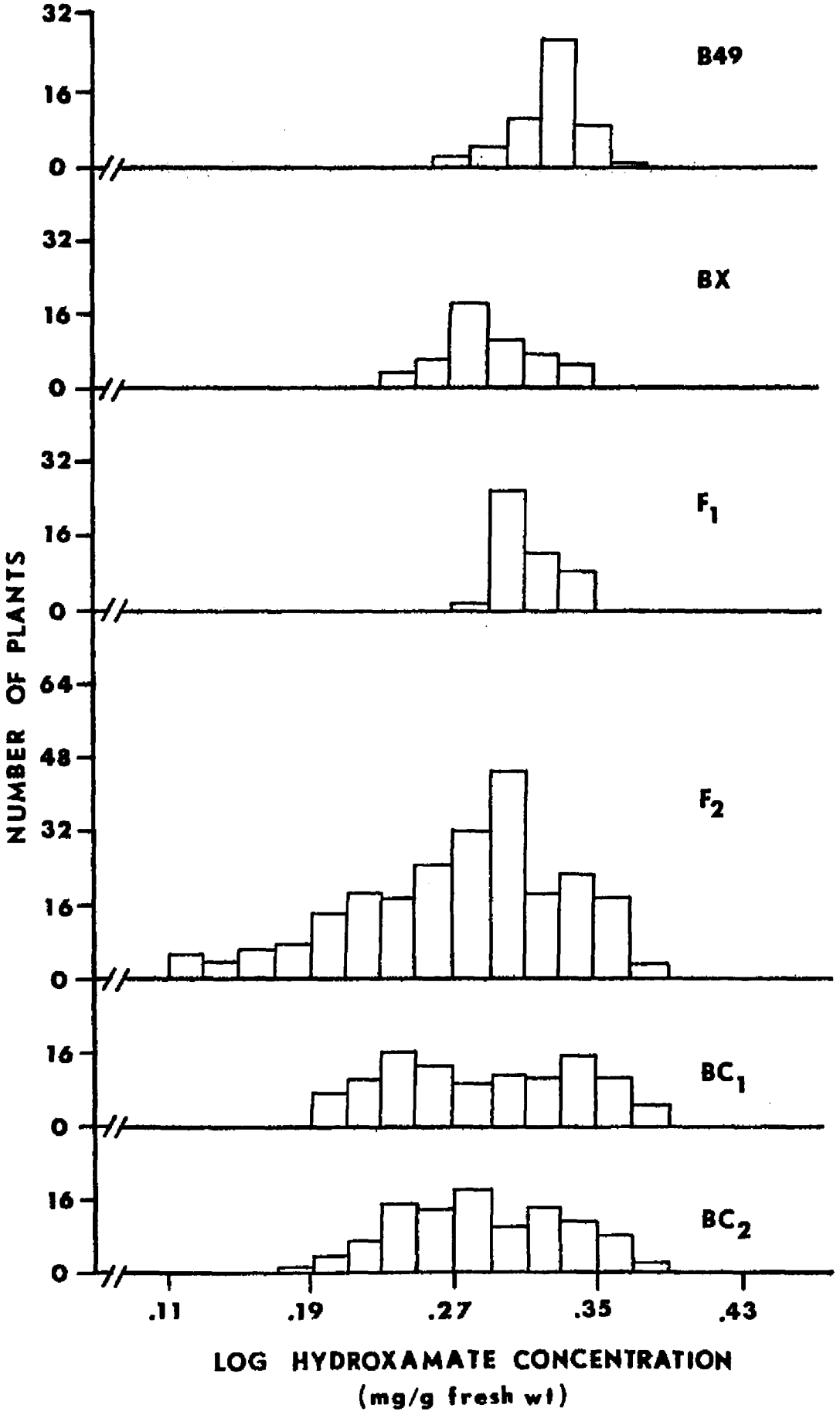


Figure 5. Frequency distributions for the parental, F_1 F_2, BC_1, and BC_2 populations for hydroxamate concentrations in the cross BxBx X B49.

concentration in B49.

Backcrosses of the F_1 to either parent resulted in mean concentrations of hydroxamates that were similar in magnitude. However, the frequency distributions for each backcross were slightly bimodal. The distribution for BC_1 (F_1 X B49) exhibited one mode at 0.19 to 0.28 mg and another mode from about 0.28 to 0.37 mg. BC_2 (F_1 X BxBx) also possessed two modes although not as easily discernible as with BC_1. These modes ranged from about 0.19 to 0.31 mg and 0.31 to 0.37 mg. The bimodal nature of the backcross distributions can be explained in part by considering the Bx gene alone. Since B49 in all probability does not possess the Bx gene, backcrosses of the F_1 to the two parents would result in the expected genotypes BxBx and Bxbx for the F_1 backcrossed to BxBx and Bxbx and bxbx for the F_1 backcrossed to B49. The addition of polygenes from B49 along with environmental effects would tend to blur these distinct differences resulting in the distributions shown in Fig. 5.

These data tend to suggest that hydroxamate concentration in BxBx X B49 results primarily from the addition of a single partially dominant gene from BxBx to the polygenes from B49.

The genetic pattern exhibited by BxBx X B37 was similar to that exhibited by BxBx X B49. BxBx averaged 0.290 mg while B37 averaged 0.125 mg hydroxamates/g fresh weight (Table 5). The relatively large deviation of the F_1 mean (0.238 mg) from the midparental value 0.204 mg indicated dominance effects.

As with BxBx X B49, the F_2 frequency distribution appeared highly skewed to the right (Fig. 6). Although it was

Table 5. Ranges, means, and variances for hydroxamate concentration in parents and progenies from the cross BxBx X B37.≠

Population	No. of Plants	Range	Mean	Variance
B37	50	0.097 - 0.158	0.125	0.000241
BxBx	48	0.243 - 0.337	0.290	0.000606
F_1	50	0.193 - 0.265	0.238	0.000234
F_2	241	0.061 - 0.312	0.191	0.004212
BC_1≠	103	0.100 - 0.324	0.215	0.003460
BC_2≠	105	0.176 - 0.342	0.257	0.001856

≠ Original data were transformed to logarithms for calculation of ranges, means, and variances.

≠ BC_1 and BC_2 = backcrosses of the F_1 to B37 and BxBx, respectively.

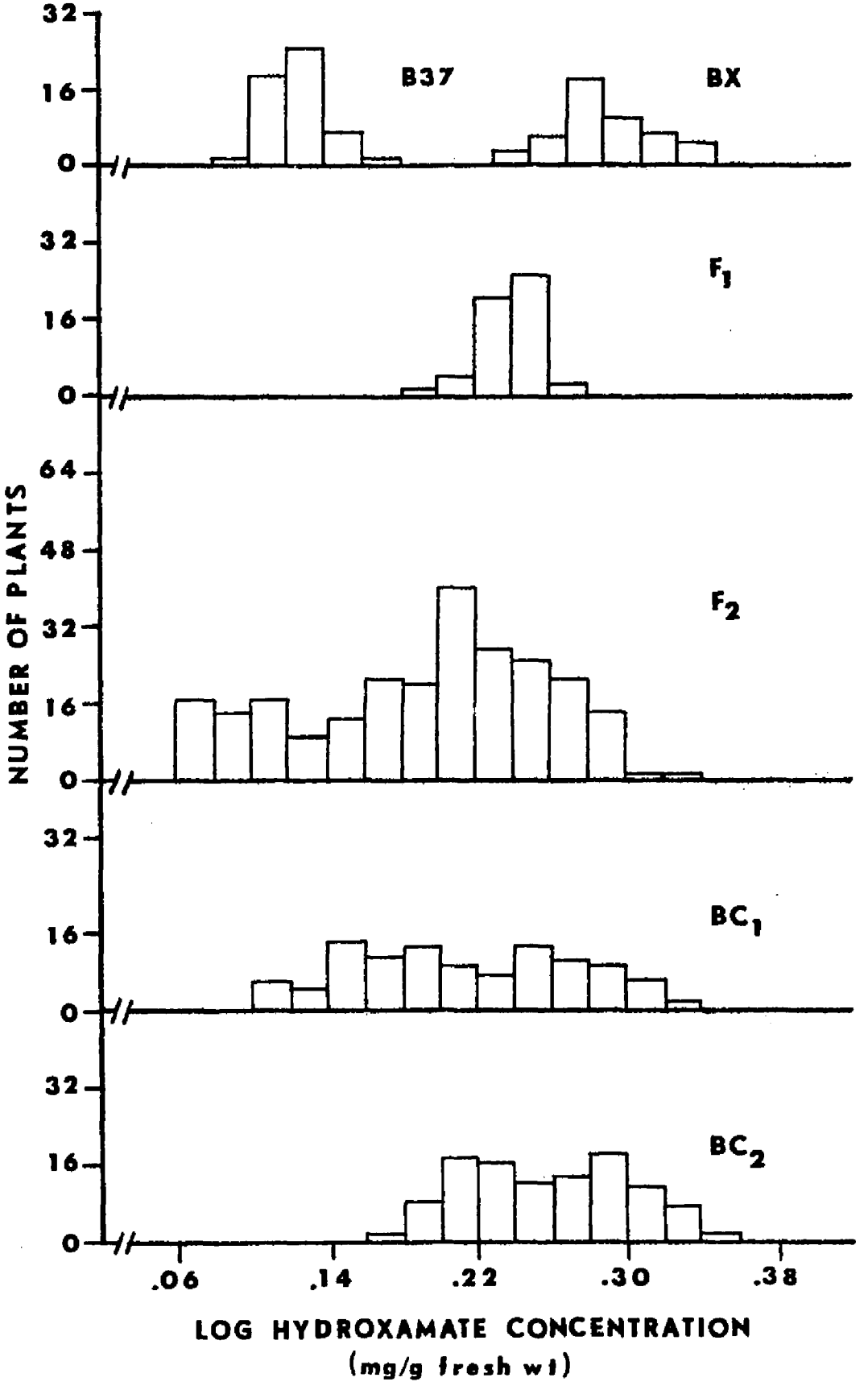


Figure 6. Frequency distributions for the parental, F_1 F_2, BC_1, and BC_2 populations for hydroxamate concentration in the cross BxBx X B37.

impossible to divide hydroxamate concentration into discrete classes, the effect of the BxBx gene was evidenced by the obvious departure of the F_2 distribution from normality. Similar trends were apparent in the two backcross populations. The frequency distributions for both BC_1 and BC_2 generations were bimodal. BC_1 appeared to possess modes ranging from about 0.10 to 0.24 mg and 0.24 to 0.36 mg while BC_2 exhibited modes ranging from about 0.16 to 0.28 mg and 0.28 to 0.36 mg.

The data from the F_2, BC_1, and BC_2 distributions suggest that hydroxamate concentration is controlled in this cross primarily by a major gene from BxBx along with a few minor genes from B37.

Variance components for hydroxamate concentration in the five selected crosses are shown in Table 6. The phenotypic variances were considerably higher for crosses involving BxBx than for crosses involving bxbx. This was probably a reflection of the dominance effects contributed by BxBx which resulted in a higher frequency of extreme genotypes in the F_2 populations. Similarly, the smaller variances exhibited by the crosses bxbx X B49 and bxbx X B37 reflect the normal distribution curves in which the majority of individuals were clustered about the means.

The environmental variances for each cross were small in comparison to the total phenotypic variances. Genetic variance therefore accounted for the majority of the phenotypic variation for this trait. In all crosses the

Table 6. Components of variance for hydroxamate concentration in selected crosses among four maize inbreds.

Cross[a]	V_P	V_A	V_D	V_E
BxBx X bxbx	8.601[b]	6.830	1.370	0.401
BxBx X B49	3.660	2.434	0.767	0.459
BxBx X B37	4.212	3.104	0.748	0.360
bxbx X B49	2.314	1.950	0.059	0.305
bxbx X B37	0.682	0.468	0.007	0.210

[a] Original data transformed to logarithms for analysis.

[b] All values X 10^{-3}.

additive genetic variance was considerably higher than the dominance variance and accounted for the majority of the genetic variation. However, dominance variation was proportionately higher in the crosses involving BxBx.

Estimates of heritability, degree of dominance, and percent dominance for hydroxamate concentration in five selected crosses are shown in Table 7. Heritability estimates ranged from 0.64 to 0.79 and reflect the high proportion of additive genetic variation to the total phenotypic variation. Based upon these estimates, selection for hydroxamate concentration by nearly any breeding method would be effective in these crosses.

Values for the degree of dominance in the five crosses ranged from 0.17 to 0.79. However it was observed that crosses involving BxBx exhibited a much higher degree of dominance than crosses involving bxbx. It is hypothesized that the inbreds B49 and B37 do not possess any gene or genes with dominance effects comparable to that exhibited by BxBx. Therefore B49 and B37 in combination with bxbx would be expected to yield the lower degree of dominance values of 0.25 and 0.17 exhibited by the crosses bxbx X B49 and bxbx X B37, respectively.

Similarly, percent dominance values were comparably higher for crosses involving BxBx than for crosses involving bxbx. This is a reflection of the higher proportion of dominance variance to the total phenotypic variation exhibited by BxBx crosses.

Table 7. Estimates of heritability, degree of dominance, and percent dominance for hydroxamate concentration in selected crosses among four maize inbreds.

Cross	Heritability	Degree of Dominance	Percent dominance to the total variation
BxBx X bxbx	0.79	0.63	16.71
BxBx X B49	0.67	0.79	23.96
BxBx X B37	0.74	0.69	19.42
bxbx X B49	0.64	0.25	2.95
bxbx X B37	0.68	0.17	1.47

These data support the hypothesis that hydroxamate concentration in BxBx is conditioned primarily by a major partially dominant gene. Hydroxamate concentration in B49 and B37 appears to be conditioned by genes with smaller effects.

Recurrent Selection

An original source population of 13 inbred lines was analyzed for hydroxamate concentration using the rapid procedure. Mean concentrations of hydroxamates in the 13 inbred lines are given in Table 8. Concentrations of hydroxamates ranged from 0.07 mg for bxbx to 1.17 mg hydroxamates/g fresh weight for CI31A. The population mean for these lines was 0.54 mg. The five inbreds CI31A, B49, BxBx, R101, and Oh45 were chosen for use in the recurrent selection program based upon their high hydroxamate content. The five inbreds averaged 0.92 mg.

The results of two cycles of recurrent selection for increasing hydroxamate concentration are shown in Fig. 7. The first cycle of recurrent selection raised the original population mean of 0.54 mg to 0.79 mg. This was an increase of about 0.25 mg. The variance of the first cycle population was 0.021. The heritability estimate (narrow sense) for the same population was estimated as 0.66. This value was within the range of heritability estimates obtained in the inheritance studies. Plants averaging 1.05 mg were chosen to produce the second cycle population.

The second cycle of recurrent selection raised the population mean from 0.79 mg to 0.93 mg. The increase of 0.14 mg

Table 8. Mean concentration of hydroxamates in 13 maize inbreds.

Inbred	Hydroxamate concentration* (mg/g fresh weight)
CI31A	1.17
B49	1.10
BxBx	.90
R101	.84
Oh45	.64
W22	.58
Oh43	.52
B52	.51
B14A	.31
Hy	.30
WF9	.28
B37	.22
bxbx	.07

* Values represent the mean of three replications with three plants/replication.

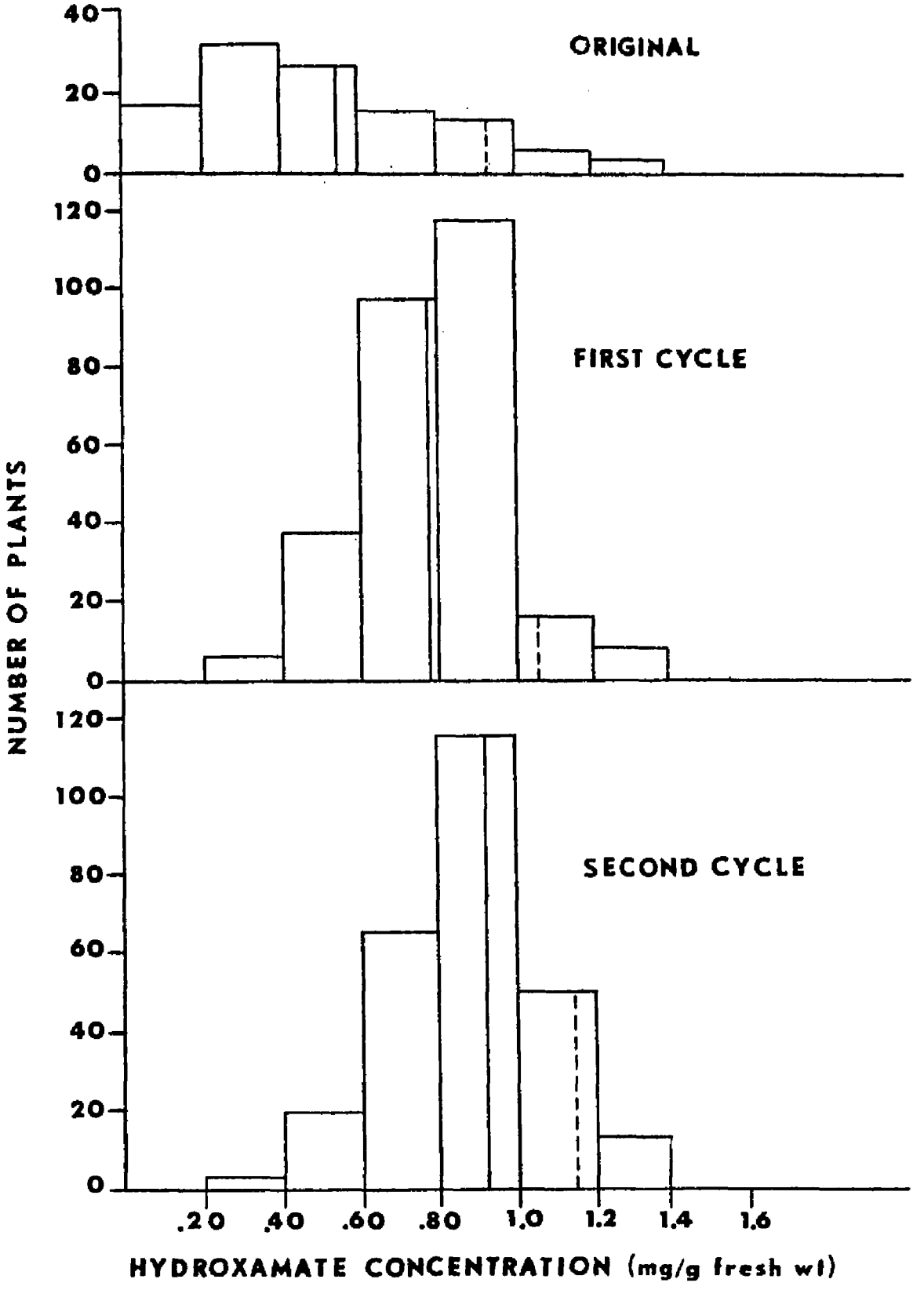


Figure 7. Two cycles of recurrent selection for increasing hydroxamate concentration in maize. In each distribution the mean is indicated by a solid vertical line and the mean of the plants selected for the next cycle by a dotted vertical line.

was about half of that produced by the first cycle of recurrent selection. Similarly, the variance of the second cycle population dropped to 0.014. The heritability estimate for the second cycle population was 0.54. Plants averaging about 1.15 mg were selected to initiate a third cycle of simple recurrent selection.

In all, two cycles of recurrent selection raised the original population mean from 0.54 to 0.93 mg. This is nearly a twofold increase in hydroxamate concentration. However, the value of 0.93 mg did not exceed the highest parental mean (CI31A = 1.17 mg). Although substantially less improvement was achieved in the second cycle as compared to the first cycle of recurrent selection, the variance by comparison was only slightly reduced. It would therefore seem likely that considerable genetic variance exists in these populations for hydroxamate concentration. On this basis it is hoped that additional cycles of recurrent selection will result in further increases in hydroxamate concentration.

SUMMARY

1. Five selected crosses among four inbred lines were used to study the inheritance of hydroxamates in maize.
2. Data from the F_1, F_2, and backcross distributions indicated that hydroxamate concentration is controlled monogenically in the cross BxBx X bxbx and multigenically in the crosses bxbx X B49 and bxbx X B37.
3. Estimates of gene number indicated that hydroxamate concentration is controlled in B49 and B37 by five and two genes, respectively.
4. Additive genetic variance was the most important component of the phenotypic variance and resulted in heritability estimates ranging from 0.64 to 0.79. However, the dominance component of variance was considerably higher for crosses involving BxBx than for the crosses bxbx X B49 and bxbx X B37. This was reflected in the high estimates of degree of dominance exhibited by the BxBx crosses.
5. In the same study two cycles of recurrent selection were performed to increase hydroxamate concentration in maize.
6. One cycle of recurrent selection increased the original population mean from 0.54 mg to 0.79 mg hydroxamates/g fresh weight. An additional cycle increased the mean to 0.93 mg.
7. Heritability estimates (narrow sense) for the two populations were calculated as $h^2 = 0.66$ and $h^2 = 0.54$, respectively.

LITERATURE CITED

(1) Allard, R. W. 1960. Principles of Plant Breeding. John Wiley and Sons, Inc., New York.

(2) Anglade, P. and P. M. Molot. 1967. Mise en evidence d'une relation entre les sensibilités de lignees de mais a la pyrale (Ostrinia nubilalis HBN.) et a l'helminthosporiose (Helminthosporium turcicum Pass.). Ann. Epiphyties 18:279-284.

(3) Barnett, R. D. and C. E. Caviness. 1968. Inheritance of hydrocyanic acid production in two sorghum x sudangrass crosses. Crop Sci. 8:89-91.

(4) Beck, S. D., E. T. Kaske and E. E. Smissman. 1957. Quantitative estimation of the resistance factor 6-methoxybenzoxazolinone in corn plant tissue. J. Agric. Food Chem. 5:933-935.

(5) Be Miller, J. N. and A. J. Pappelis. 1965. 2-4-Dihydroxy-7-methoxy-1,4-benzoxazin-3-one glucoside in corn. I. Relation of water soluble, 1-butanol-soluble glucoside fraction content of pith cores and stalk rot resistance. II. Isolation of 6-methoxy-2(3)-benzoxazolinone fraction as a measure of glucoside content and tissue difference of glucoside content. Phytopathology 55:1237-1243.

(6) Brim, C. A. and C. W. Stubr. 1973. Application of genetic male sterility to recurrent selection schemes in soybeans. Crop Sci. 13:528-530.

(7) Bowman, M. C., M. Berosa and J. A. Klun. 1968. Spectro-photofluorometric determination of 6-methoxy-2(3)-benzoxazolinone, an indicator of resistance to European corn borer in Zea mays. J. Econ. Entomol. 61: 120-123.

(8) Carangal, V. R., S. M. Ali, A. F. Koble, E. H. Rinke, and J. C. Sentz. 1971. Comparison of S_1 and test cross evaluation for recurrent selection in maize. Crop Sci. 11:658-661.

(9) Castle, W. E. 1921. An improved method of estimating the number of genetic factors concerned in cases of blending inheritance. Science 54:223.

(10) Charles, D. R. and H. H. Smith. 1939. Distinguishing between two types of gene action in qualitative inheritance. Genetics 24:34-38.

(11) Comstock, R. E. and H. F. Robinson. 1952. Genetic parameters, their estimation and significance. Proc. Sixth Intern. Grasslands Congr. 284-291.

(12) Comstock, R. E., H. F. Robinson and P. H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. Jour. 41:360-367.

(13) Couture, R. M., D. G. Routley and G. M. Dunn. 1970. Role of cyclic hydroxamic acids on monogenic resistance to Helminthosporium turcicum in maize. Maize Genet. Coop. News Lett. 44:169-170.

(14) _____, _____ and _____. 1971. Role of cyclic Hydroxamic acids and monogenic resistance of maize to Helminthosporium turcicum. Physiol. Plant Pathology 1:515-521.

(15) Duclos, L. A. and P. H. Crane. 1968. Comparative performances of top crosses and S_1 progeny for improving populations of corn (Zea mays L.). Crop Sci. 8: 191-194.

(16) Dudley, J. W. and R. H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9:257-262.

(17) East, E. M. 1916. Studies on size inheritance in Nicotiana. Genetics 1:164-176.

(18) East, E. M. and D. F. Jones. 1920. Genetic studies on the protein content of maize. Genetics 5:543-610.

(19) Eberhart, S. A., Seme Debela and A. R. Hallauer. 1973. Reciprocal recurrent selection in the BSSS and BSCB1 maize populations and half-sib selection in BSSS. Crop Sci. 13:451-456.

(20) Elnaghy, M. A. and P. Linko. 1962. The role of 4-0-glucosyl- 2,4-dihydroxy-7- methoxy-1,4-benzoxazin-3-one in resistance of wheat to stem rust. Physiol. Plant 15:764-771.

(21) Elnaghy, M. A. and M. Shaw. 1966. Correlation between resistance to stem rust and the concentration of glucoside in wheat. Nature 210:417-418.

(22) Falconer, D. S. 1960. Introduction to Quantitative Genetics. Ronald Press Co., New York. 365pp.

(23) Fisher, R. A. 1918. The correlations among relatives on the supposition of mendelian inheritance. Trans. Royal Soc. of Edenburgh LII: 399-433.

(24) Genter, C. F. and M. W. Alexander. 1962. Comparative performance of S_1 progenies and test crosses of corn. Crop Sci. 2:516-519.

(25) Genter, C. F. 1973. Comparison of S_1 and test cross evaluation after two cycles of recurrent selection in maize. Crop Sci. 13:524-527.

(26) Griffing, J. B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Austral. Jour. Biol. Sc. 9:463-493.

(27) Hallauer, A. R. 1970. Genetic variability for yield after four cycles of reciprocal recurrent selection in maize. Crop Sci. 10:482-485.

(28) _____. and S. A. Eberhart. 1970. Reciprocal full-sib selection. Crop Sci. 10:315-316.

(29) Hamilton, R. H. 1964. Tolerance of several grass species to 2-chloro-s-triazine herbicides in relation to degradation and content of benzoxazolinone derivatives. J. Agric. Food Chem. 12:14-17.

(30) _____. 1964. A corn mutant deficient in 2, 4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one with an altered tolerance of atrazine. Weeds 12:27-31.

(31) Hayes, H. K. and R. J. Garber. 1919. Synthetic production of high protein corn in relation to breeding. Jour. Amer. Soc. Agron. 11:309-318.

(32) Hayman, B. I. 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.

(33) Horner, E. S., W. H. Chapman, H. W. Lundy and M. C. Lutrick. 1972. Commercial utilization of the products of recurrent selection for specific combining ability in maize. Crop Sci. 12:602-604.

(34) Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. Jour. Amer. Soc. Agron. 37:134-145.

(35) Jenkins, M. T. 1935. The effect of inbreeding and selection within inbred lines of maize upon the hybrids made after successive generations of selfing. Iowa State Coll. Jour. Sci. 9:429-450.

(36) _____. 1940. The segregation of genes affecting yield of grain in maize. Jour. Amer. Soc. Agron. 32:55-63

(37) _____, A. L. Robert and W. R. Findley, Jr. 1954. Recurrent selection as a method for concentrating genes for resistance to Helminthosporium turcicum leaf blight in corn. Agron. Jour. 46:89-94.

(38) Jinahyon, S. and W. A. Russell. 1969. Evaluation of recurrent selection for stalk-rot resistance in an open-pollinated variety of maize. Iowa State J. Sci. 43:229-237.

(39) Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:767-788.

(40) _____. 1956. The F_2 and backcross generations from a set of diallel crosses. Heredity 10:1-30.

(41) Johannson, W. 1909. Elemente der exakten Erblich Keitslehre. Jena:Gustav Fischer.

(42) Jones, L. P., W. A. Compton and C. O. Gardener. 1971. Comparison of full and half sib reciprocal recurrent selection. Theo. Appl. Genet. 41:36-39.

(43) Kempthorne, O. and O. B. Tandon. 1953. The estimation of heritability by regression of offspring on parent. Biometrics 9:90-100.

(44) Klun, J. A. and T. A. Brindley. 1966. Role of 6-methocy-benzoxazolinone in inbred resistance of host (maize) to first brood larvae of European corn borer. J. Econ. Entomol. 59:711-718.

(45) _____, C. L. Tipton, and T. A. Brindley. 1967. 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), an active agent in the resistance of maize to European corn borer. J. Econ. Entomol. 60:1529-1533.

(46) _____, W. D. Guthrie, A. R. Hallauer and W. A. Russell. 1970. Genetic nature of the concentration of 2,4-dihydroxy-7-methoxy 2H-1,4-benzoxazin-3(4H)-one and resistance to European corn borer in a diallel set of eleven maize inbreds. Crop Sci. 10:87-90.

(47) Knott, D. R. and J. Kumar. 1972. Tests of the relationship between a specific phenolic glucoside and stem rust resistance in wheat. Physiol. Plant Path. 2:393-399.

(48) Liang, G. H. L. and T. L. Walter. 1968. Heritability estimates and gene effects for agronomic traits in grain sorghum, Sorghum vulgare Pers. Crop Sci. 8:77-81.

(49) Long. B. J., G. M. Dunn and D. G. Routley. 1974. Rapid procedure for estimating cyclic hydroxamate (DIMBOA) concentration in maize. Crop Sci. 14:601-603.

(50) _____. 1975. Relationship of hydroxamic acid content and resistance to northern corn leaf blight. Crop Sci. 15: 333-335.

(51) _____. 1976 Relationship of hydroxamic acid content in maize and resistance to the corn leaf aphid. Crop Sci. 17: 55-58.

(52) Lonnquist, J. H. 1951. Recurrent selection as a means of modifying combining ability in corn. Agron. Jour. 43:311-315.

(53) _____. 1968. Further evidence of testcross versus line performance in maize. Crop Sci. 8:50-53.

(54) Lush, J. L. 1945. Animal Breeding Plans. Iowa State College Press, Ed. 3. 443 pp.

(55) Mather, K. 1949. Biometrical Genetics. Methuen and Co., London. 162 pp.

(56) Mock, J. J. and S. H. Schuetz. 1974. Inheritance of tassel branch number in maize. Crop Sci. 14:885-888.

(57) Moll, R. H. and C. W. Stuber. 1971. Comparisons of response to alternative selection procedures initiated with two populations of maize (Zea mays L.). Crop Sci. 11:706-711.

(58) Panse, V. G. 1940. The application of genetics to plant breeding- II. The inheritance of quantitative characters and plant breeding. Jour. Genetics 40: 283-302.

(59) Penny, L. H., W. A. Russell and G. F. Sprague. 1962. Types of gene action in yield heterosis in maize. Crop Sci. 2:341-344.

(60) _____, G. E. Scott and W. D. Guthrie. 1967. Recurrent selection for European corn borer resistance in maize. Crop Sci. 7:407-408.

(61) _____, and S. A. Eberhart. 1971. Twenty years of reciprocal recurrent selection in the BSS and BSCB1 maize populations and half-sib selection in BSSS. Crop. Sci. 13:451-456.

(62) Powers. L. 1942. The nature of the series of environmental variances and the estimation of the genetic variances and the geometric means of crosses involving species of Lycopersicon. Genetics 27:561-575.

(63) Riggs, T. J. and A. M. Hayter. 1972. Diallel analysis of the time to heading in spring barley. Heredity 29:341-357.

(64) Sampson, D. R. 1971. Additive and non-additive genetic variances and genotypic correlations for yield and other traits in oats. Can. J. Genet. Cytol. 13: 864-872.

(65) _____ and E. E. Rosenkrantz. 1974. Effectiveness of recurrent selection for corn stunt resistance in a maize variety. Crop Sci. 14:758-760.

(66) Singh, S. M. and K. Lesins. 1971. Genetic nature of two indexes of compatibility in alfalfa. Can. J. Genet. Cytol. 13:51-54.

(67) Sprague, G. F. and B. Brimhall. 1950. Relative effectiveness of two systems of selection for oil content of the corn kernel. Agron. Jour. 42:83-88.

(68) _____, W. A. Russell and L. H. Penny. 1959. Recurrent selection for specific combining ability and type of gene action involved in yield heterosis in corn. Agron. Jour. 51:392-394.

(69) Subandi and W. A. Compton. 1974. Genetic studies in an exotic population of corn (Zea mays L.) grown under two plant densities. Theor. Appl. Genetics. 44:153-159.

(70) Thompson, D. L. 1972. Recurrent selection for lodging susceptibility and resistance in corn. Crop Sci. 12:631-634.

(71) Virtanen, A. I. and P. K. Hietala. 1960. Precursors of benzoxazolinone in rye plants. I. Precursor II, the aglucone. Acta Chem. Scand. 14:499-502.

(72) Wahlroos, O. and A. I. Virtanen. 1959. The precursors of 6-methoxy-benzoxazolinone in maize and wheat plants, their isolation and some of their properties. Acta Chem. Scand. 13:1906-1908.

(73) Walton, P. D. 1971. The genetics of yield in spring wheat (Triticum aestivum L.). Can J. Genet. Cytol. 13:110-114.

(74) Warner, J. N. 1952. A method for estimating heritability. Jour. Agron. 44:427-430.

(75) Wesenberg, D. M. and H. L. Shands. 1973. Heritability of oat caryopsis percentage and other grain quality components. Crop Sci. 13:481-484.

(76) Widstrum, N. W., W. J. Wiser and L. F. Bauman. 1970. Recurrent selection for earworm resistance. Crop Sci. 10:674-676.

BIOGRAPHICAL DATA

Name in Full: Bryant Jerome Long

Date of Birth: June 26, 1950

Place of Birth: Bryan, Ohio

Secondary Education:

Bryan High School, Bryan, Ohio

Collegiate Institutions Attended:	Dates	Degree
Kent State University	1968 - 1969	
Defiance College	1969 - 1972	B.S.
University of New Hampshire	1972 - 1974	M.S.
University of New Hampshire	1974 - 1977	Ph.D.

Publications:

1. Calub, A. G., B. J. Long, and G. M. Dunn. 1974. Production of inhibitory compounds in corn inbreds with monogenic and multigenic resistance to Helminthosporium turcicum. Crop Sci. 14:303-304.

2. Long, B. J. 1974. Relationship of hydroxamic acid content in maize and resistance to northern corn leaf blight. M.S. Thesis. University of New Hampshire.

3. Long, B. J., G. M. Dunn, and D. G. Routley. 1974. Relation of hydroxamic acid content (DIMBOA) to resistance to Helminthosporium turcicum. Maize Genetics Cooperation News Letter 48:131.

4. Long, B. J., G. M. Dunn, and D. G. Routley. 1974. Rapid procedure for estimating cyclic hydroxamate (DIMBOA) in maize. Crop Sci. 14: 601-603.

5. Long, B. J., G. M. Dunn, and D. G. Routley. 1975. Relationship of hydroxamic content in maize and resistance to northern corn leaf blight. Crop Sci. 13:333-335.

6. Long, B. J., G. M. Dunn, J. S. Bowman, and D. G. Routley. 1976. Relation of hydroxamic acid concentration (DIMBOA) to resistance to the corn leaf aphid. Maize Genetics Cooperation News Letter 50:91.

7. Long, B. J., G. M. Dunn, J. S. Bowman, and D. G. Routley. 1976. Relationship of hydroxamic acid content in maize and resistance to the corn leaf aphid. Crop Sci. 17:55-58.

8. Long, B. J., G. M. Dunn, and D. G. Routley. 1976. Two cycles of recurrent selection for increasing hydroxamate concentration in maize. Maize Genetics Cooperation News Letter 51:70-71.

9. Long, B. J.. G. M. Dunn, and D. G. Routley. 1976. Relation of hydroxamate concentration to resistance to Helminthosporium turcicum in the field. Maize Genetics Cooperation News Letter 51:71.

Positions Held:	Dates
1. Graduate Research Assistant Department of Plant Science University of New Hampshire Durham, New Hampshire	Sept., 1972 - June, 1977